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EVERGREEN AND DECIDUOUS FERNS OF THE COAST REDWOOD FOREST

EMILY E. BURNS
Save the Redwoods League, 111 Sutter Street, 11th Floor, San Francisco, CA 94104
eburns@savetheredwoods.org

JARMILA PITTERMANN
Department of Ecology and Evolutionary Biology, University of California,
Santa Cruz, CA 95064

CHRISTOPHER RICO
DuPont Pioneer, 18369 County Rd 98, Woodland, CA 95695

ABSTRACT

The understory of California's coast redwood forests boasts an abundance of ferns, half of which are drought deciduous. Despite their ecological importance, little is known about the functional differences between deciduous and perennial ferns. This study explored morphological and physiological leaf traits of an assortment of coast redwood forest fern species sampled from the southern, drier extent of the ecosystem, to determine if deciduous species are less drought tolerant than co-occurring evergreen species because of their shorter leaf lifespan. In mid-summer, all ferns were well hydrated with water potentials above –1 MPa. Although the deciduous ferns were more vulnerable to hydraulic dysfunction by embolism, it is likely that all species experienced similarly low degrees of embolism *in situ*, as inferred from mid-day water potential measurements. Despite their similar water relations when water was not limiting, we observed that deciduous ferns had thinner pinnae because they avoid the late summertime drought by shedding their fronds, in contrast to co-occurring evergreen ferns that invest in sclerophyllous leaves that persist for at least two growing seasons. Our study shows that even within the mesic habitat of the forest understory, ferns can exploit a spectrum of functional strategies that allows them to thrive in separate niches, differences that may become more pronounced in water-limiting habitats.

Key Words: embolism, hydraulic conductivity, leaf allometry, pteridophytes, stomatal conductance, water potential, xylem.

Evergreen plants dominate many ecosystems around the world (Axelrod 1966; DeFries et al. 2000) and in California, where the drought season is limited to less than four months (Mooney and Dunn 1970), evergreens comprise more than 75% of the flora in mesic habitats. By continuously retaining leaves, evergreens benefit from an extended growing season relative to deciduous species that shed their leaves for part of the year in response to seasonal water deficit (Chabot and Hicks 1982; Van Buskirk and Edwards 1995). When drought conditions are prolonged however, deciduous plants benefit from reduced respiratory costs and better water conservation in perennial stem and root tissues by eliminating their leaf area (Mooney and Dunn 1970; Chabot and Hicks 1982; Givnish 2002; Westoby et al. 2002). Interestingly, evergreen and deciduous species can retain leaves for varying lengths of time while occupying the same habitat and sharing the same access to water (Wright et al. 2004; Brodribb and Holbrook 2005). Given this variation in life history strategies, can co-occurring deciduous and evergreen plants vary in drought tolerance?

The coast redwood (*Sequoia sempervirens* [D. Don] Endl.) forests of Northern California host abundant populations of deciduous and evergreen ferns, which often grow side-by-side. Specifically, there are 16 species of shallowly rooted, shade-tolerant species with differing leaf retention strategies (Waring and Major 1964; Grillos 1966). These ferns perennially blanket the forest floor, stream banks, and decomposing logs (Lyons et al. 1988). Ferns typically root in the upper soil layer (Limm 2009), and since the coastal California climate is categorized as Mediterranean with wet winters and low-precipitation summers, water may become limiting in this shallow soil stratum. This is especially relevant after the rainy season when moisture declines and summertime air temperatures increase (Ewing et al. 2009). Half of the coast redwood fern species are drought deciduous and yet surprisingly, little is known about how these ferns with short-lived leaves differ physiologically and morphologically from the evergreen species with which they co-occur.

While coast redwood forest ferns all produce new leaves during the wet season (November to April), the timing of leaf shedding varies by species. Evergreen species including *Polystichum munitum* (Kaulf.) C. Presl (Western sword fern), *Woodwardia fimbriata* Sm. (giant chain fern), and *Dryopteris arguta* (Kaulf.) Maxon (wood fern) retain each leaf cohort produced in the spring for more than two years. They maintain multiple leaf cohorts year-

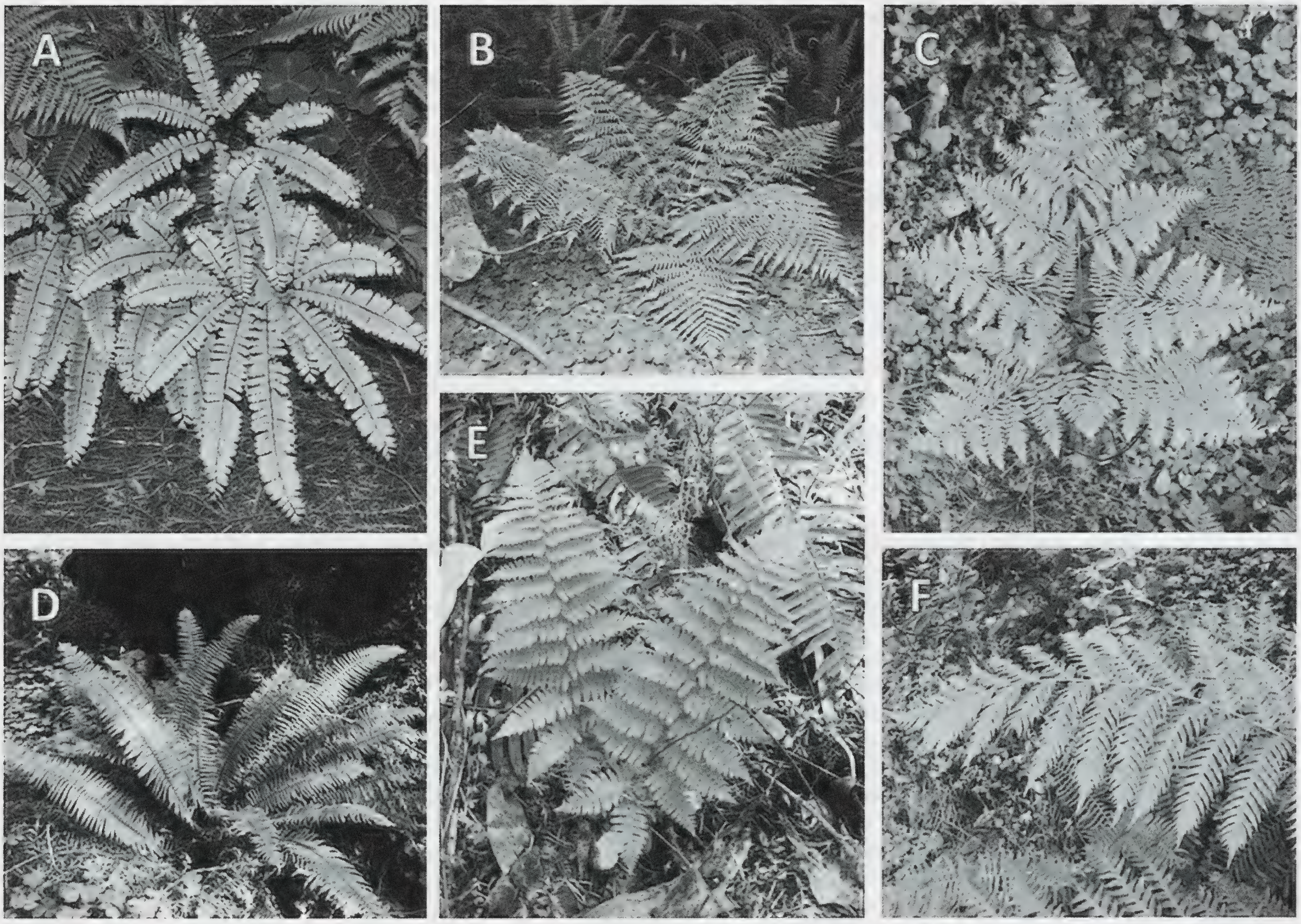

FIG. 1. Diversity of leaf types in ferns studied in southern coast redwood forests range from deciduous, A. *Adiantum aleuticum*, B. *Athyrium filix-femina*, and C. *Pteridium aquilinum*, to evergreen, D. *Polystichum munitum*, E. *Dryopteris arguta*, and F. *Woodwardia fimbriata* for leaves sampled at the Landels-Hill Big Creek Reserve and University of California, Santa Cruz Natural Reserve.

round and only the oldest cohort senesces at the end of each dry season (September to October). In contrast, deciduous species including *Adiantum aleuticum* (Rupr.) C.A. Paris (five-finger fern), *Athyrium filix-femina* (L.) Roth (lady fern), and *Pteridium aquilinum* L. Kuhn (bracken fern) display only one leaf cohort at a time and exhibit crown senescence by the end of each annual dry season. While deciduous ferns ultimately avoid drought through leaf shedding, they do retain leaves through part of the drought season.

This study explored morphological and physiological leaf characteristics of common deciduous and evergreen coast redwood forest ferns to determine if deciduous species exhibit less drought tolerance than co-occurring evergreen species because of their shorter leaf lifespan. Given that evergreen ferns retain foliage year-round regardless of the drought season duration or intensity, it was hypothesized that that long-lived fern leaves would be thicker and have xylem more able to resist hydraulic failure by air entry (cavitation) than shorter-lived leaves that are not constrained by foliar retention throughout the summer.

METHODS

The six most abundant fern species (Fig. 1) in the driest, southern extent of the coast redwood range were compared to test the hypothesis that deciduous ferns exhibit less drought tolerance than evergreen ferns. Measurements were taken mid-summer in the rainless season in order to sample fern baseline physiological responses to declining soil water availability on mature leaf cohorts for all species, but before any drought-induced senescence began in the deciduous species.

Site Descriptions

All ferns were sampled within 50 m of stream edge on alluvial terraces within closed-canopy coast redwood forests (understory PAR = 5–350 μmol) at the southern end of the ecosystem range. Evergreen species *P. munitum* and *W. fimbriata* and deciduous species *P. aquilinum* and *A. aleuticum* were measured at the Landels-Hill Big Creek Reserve (36°4′30.55″N, 121°35′24.73″W) in Monterey County at an elevation of 89 m. Evergreen *D. arguta* and deciduous *A. filix-femina* were measured at the University of California, Santa Cruz Natural Reserve (36°59′25″N, 122°3′31″W) at an elevation of 179 m. Thirty-year averages from the PRISM Climate Group (2004) show the Landels-Hill study site has similarly moderate air temperature (t_{mean} = 14.7°C; t_{min} = 9.5°C; t_{max} = 20.0°C) to the Santa Cruz site (t_{mean} = 14.5°C; t_{min} = 7.6°C; t_{max} = 21.4°C). In addition, both sites have similar total annual precipitation (Landels-Hill = 765 mm; Santa Cruz = 1121 mm) that falls primarily between October and May and negligible rainfall was measured in July (<1 mm) when the sampling occurred.

Physiology

Physiological variables were measured on ten randomly selected ferns of each species in July 2010 and 2011, a mid-summer month that represents the optimal period when little to no rain falls, soil moisture is declining (Ewing et al. 2009), but before deciduous ferns exhibit physiological decline associated with senescence. Measurements were conducted mid-day, between 1100 and 1300 hr, to assess plant dry-season water stress during the time of day when demand for water was likely greatest. Mid-rachis leaf water potential (ψ_{leaf}) was measured with a Scholander Pressure Chamber (PMS Instruments, Corvallis, OR). Concurrently on the same individuals, leaf stomatal conductance was measured to water vapor (g_s) using a steady state diffusion porometer (Model SC-1, Decagon Devices, Inc., Pullman, WA) calibrated prior to measurements. Species differences were analyzed using Analysis of Variance and Tukey's HSD using JMP software (SAS Institute Inc., San Francisco, CA).

Frond Morphology

Twenty herbivory-free leaves of each species from separate individuals (n = 120) were sampled to represent the full range of mature leaf sizes at each site to determine the allometric relationship between leaf blade length and area. The rachis length of each leaf (stipe excluded) was measured and the combined projected leaf area of the pinnae and rachis (a) was determined digitally using the software ImageJ (Rasband 2007–2012). The software SigmaPlot 12.0 (SYSTAT Software, San Jose, CA) was used to fit a non-linear equation for each species.

The leaf samples were subsequently dried at 60°C for 72 hr and the dry mass of the rachis and pinnae was measured (m, kg). Specific leaf area (SLA) was calculated as

$$\mathrm{SLA} = a/m,$$

where a (m^2) is the leaf area as determined by scanning the leaves and measuring area using ImageJ software (Garnier et al. 2001; Rasband 2007–2012). Species differences were analyzed using Analysis of Variance and Tukey's HSD using JMP software (SAS Institute Inc., San Francisco, CA).

Hydraulic Measurements

Hydraulic measurements were conducted on the stipe (petiole) of each fern frond. Stipe segments of 18–20 cm in length were sampled from eight fronds per species from separate individuals that were collected in the field, re-cut underwater to a length of 142 mm, and the ends were shaved smooth with a razor blade. Xylem emboli were removed by degassing submerged stipes overnight under vacuum in distilled water and filtered 20 mM KCl solution (0.22 μm; E-Pure filtration system; Barnstead International, Dubuque, IA). Stipes were mounted on a tubing apparatus and hydraulic conductivity (K) was measured gravimetrically under a pressure of 6–8 kPa using filtered 20 mM KCl solution following the method of Sperry (1993; see also Baer et al., 2016). The average background flow measured (the flow rates observed without a pressure head, both before and after each gravimetric flow measurement) was subtracted from the pressure-induced flow in order to improve accuracy and K was calculated as the flow rate for a given pressure gradient standardized per unit of stipe length. To calculate xylem specific conductivity (K_s), the total xylem area was measured for each stipe by cutting a thin cross-section of the distal end of each stipe segment with a razor blade, staining in phloroglucinol to highlight lignified tissue including xylem, photographing under 100–200× magnification with a digital camera mounted on a Motic BA400 compound microscope (JH Technologies, San Jose, CA), and analyzing the xylem area using ImagePro software (Media Cybernetics, Carlsbad, CA). To calculate leaf-area specific conductivity (K_{leaf}), frond pinnae were scanned and the leaf area was measured using ImageJ software. K_s and K_{leaf} were obtained by dividing K by xylem and leaf area, respectively.

The vulnerability of each species to cavitation in response to a range of xylem pressures was evaluated using the centrifuge method (Pockman et al. 1995; Alder et al. 1997). Stipes were placed securely in a custom rotor designed to fit a Sorvall RC-5C centrifuge (Thermo Fisher Scientific, Waltham, MA) and spun for three min at speeds that induce a known xylem pressure (P_x). Immediately after spinning, K was measured and used to calculate the per cent loss of conductivity (PLC) caused by centrifugation at each P_x, relative to the maximum conductivity after degassing (K_{max}) at $P_x = 0$ MPa, such that,

$$\mathrm{PLC} = 100 \times (1 - K/K_{max}),$$

where K_{max} was determined at $P_x = 0$ MPa following degassing. The stipe segments were spun progressively to more negative P_x at –0.5 MPa increments until the PLC exceeded 90%, or the most negative P_x achievable by the centrifuge at $P_x = -10$ MPa, was reached.

Vulnerability curves were measured on eight stipes per species. A Weibull function (Neufeld et al. 1992)

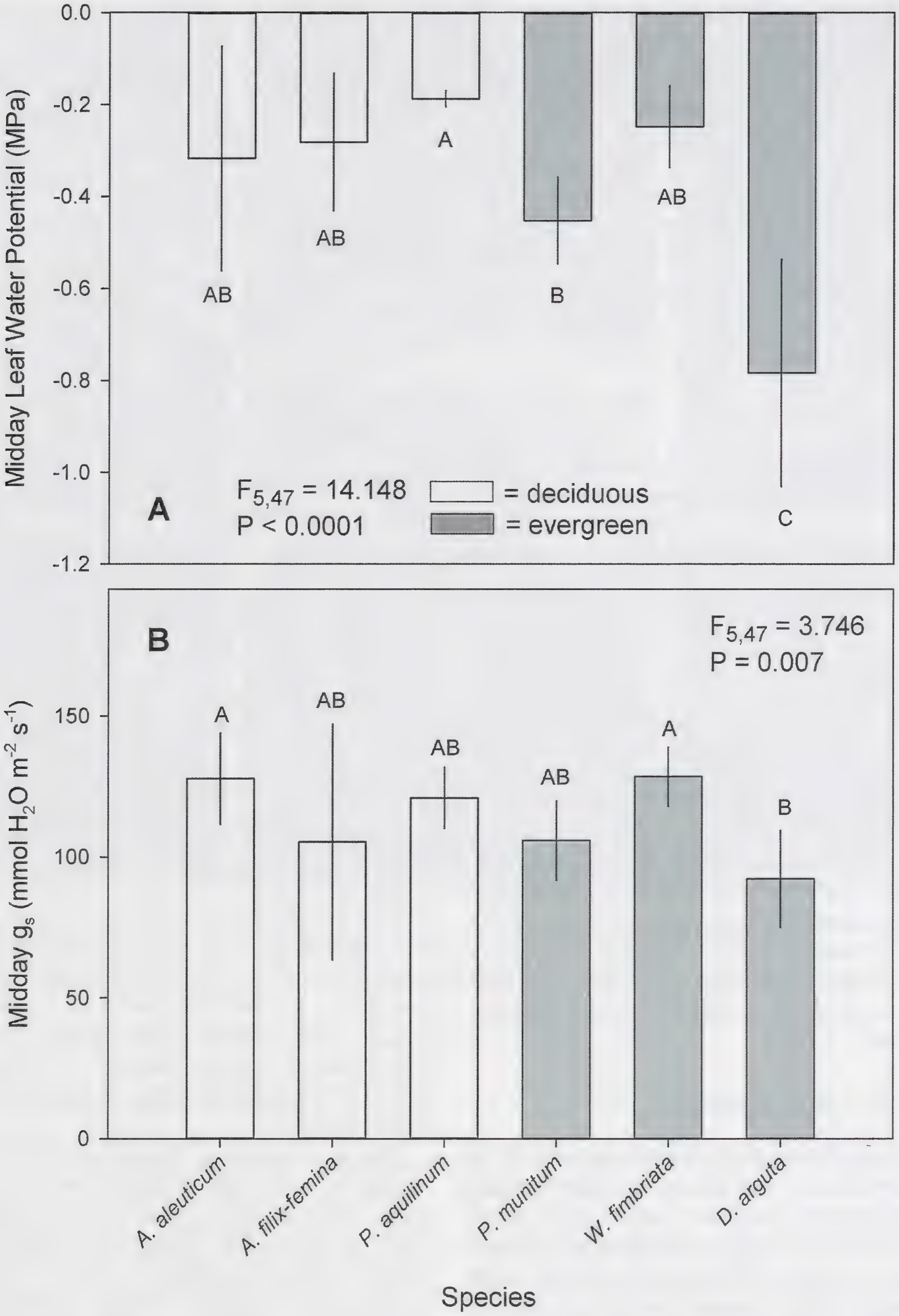

FIG. 2. A. The mean (±SD) midday leaf water potential and B. mean (±SD) midday stomatal conductance (g_s). Measurements were taken in mid-summer at the Landels-Hill Big Creek Reserve (*Adiantum aleuticum*, *Pteridium aquilinum*, *Polystichum munitum*, and *Woodwardia fimbriata*) and University of California, Santa Cruz Natural Reserve (*Athyrium filix-femina*, and *Dryopteris arguta*).

was fit to the pooled vulnerability curve data for each species using statistical software (R Core Team 2016) and the fit was used to calculate the 12%, 50%, and 88% losses of conductivity (P_{12}, P_{50}, P_{88}).

RESULTS

Physiology

Field measures of midday ψ_{leaf} and g_s indicated how hydrated and physiologically active these ferns were during midsummer (Fig. 2). The observed ψ_{leaf} values at midday indicated all species were well-hydrated. Across taxa, ψ_{leaf} ranged from –0.2 ± 0.01 MPa (mean ± standard deviation) in *Pteridium aquilinum* to –0.8 ± 0.2 MPa in *D. arguta* (Fig. 2A). All ferns exhibited measurable g_s without evidence of mid-day suppression that can occur with low water availability, with values ranging from 92 ± 17 mmol m^{-2} s^{-1} in *D. arguta* to 127.81 ± 16 mmol m^{-2} s^{-1} in *A. aleuticum* (Fig. 2B). While there were statistically significant differences in ψ_{leaf} ($F_{5,47}$ = 14.148, $p < 0.0001$) and g_s ($F_{5,47} = 3.746$, $p = 0.007$)

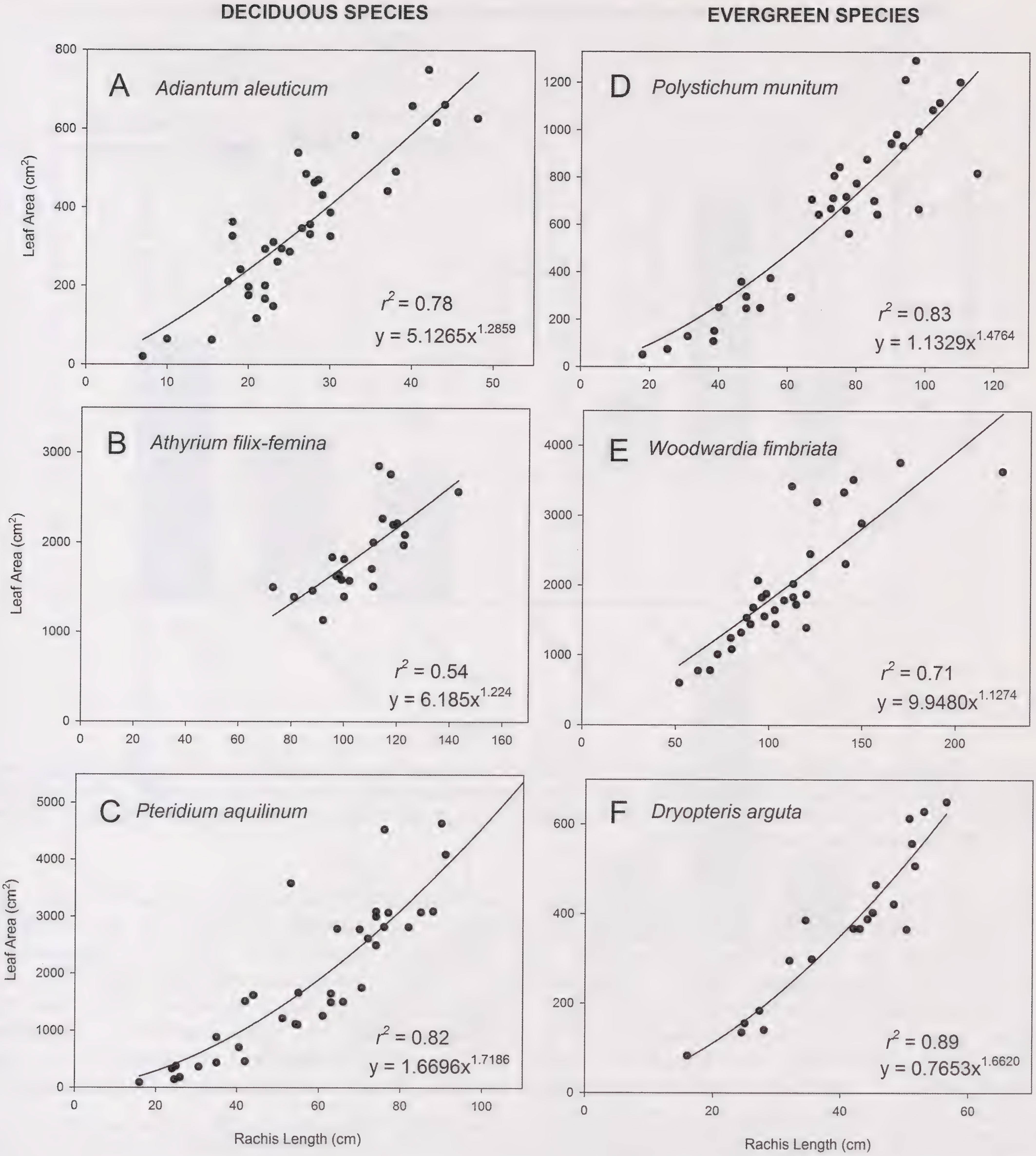

FIG. 3. The nonlinear relationship between leaf area and rachis length for A. *Adiantum aleuticum*, B. *Athyrium filix-femina*, C. *Pteridium aquilinum*, D. *Polystichum munitum*, E. *Woodwardia fimbriata*, and F. *Dryopteris arguta* for leaves sampled at the Landels-Hill Big Creek Reserve and University of California, Santa Cruz Natural Reserve.

between species, deciduous species as a group did not exhibit significantly higher ψ_{leaf} or g_s than evergreen species (Fig. 2).

Frond Morphology

Leaves of all six species exhibited a nonlinear relationship between rachis length and leaf area (Fig. 3A–F) and neither evergreen nor deciduous species had leaves much larger or smaller than the other. In fact, *W. fimbriata* (evergreen) and *P. aquilinum* (deciduous) had the largest leaves by leaf area and *A. aleuticum* (deciduous) and *D. arguta* (evergreen) had the smallest. SLA varied significantly among species ($F_{5,69} = 31.583$, $p < 0.0001$), with thinner leaves observed in the three deciduous species, *A. aleuticum*, *A. filix-femina*, and *P. aquilinum* (Fig. 4).

Hydraulic Measurements

While K_s and K_{leaf} varied significantly among species (Fig. 5A, $F_{5,44} = 9.686$, $p < 0.0001$; Fig. 5B,

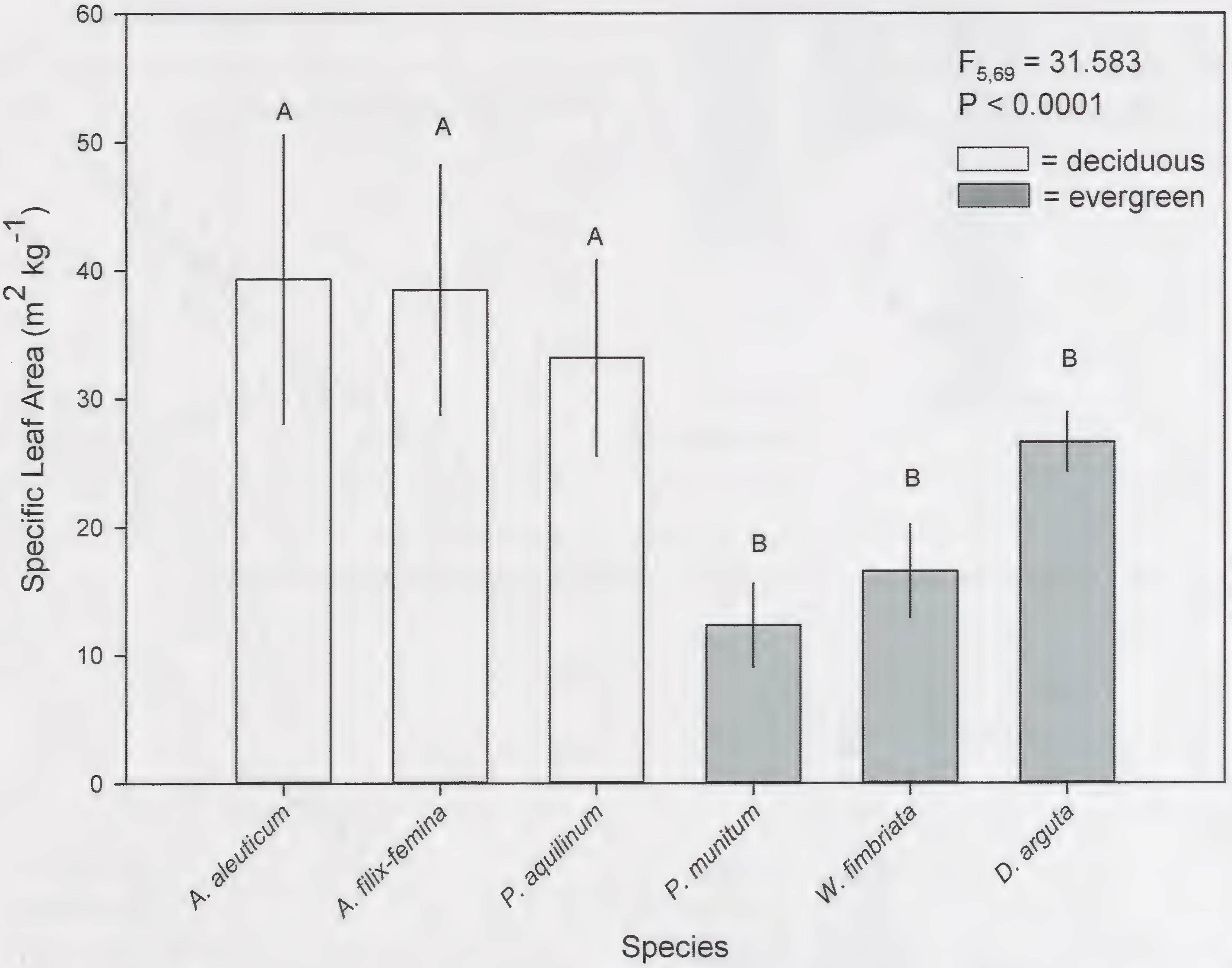

FIG. 4. The mean (±SD) specific leaf area for deciduous and evergreen species sampled at the Landels-Hill Big Creek Reserve (*Adiantum aleuticum*, *Pteridium aquilinum*, *Polystichum munitum*, and *Woodwardia fimbriata*) and University of California, Santa Cruz Natural Reserve (*Athyrium filix-femina* and *Dryopteris arguta*). Species with the same letter are not significantly different (Tukey's HSD, $\alpha = 0.05$).

$F_{5,36} = 17.77$, $p < 0.0001$), deciduous species as a group did not exhibit higher K_s than evergreen species.

Analyses of the vulnerability curves (Fig. 6) revealed that deciduous species have P_{12} values that ranged from a high vulnerability of –0.2 MPa in *A. filix-femina* to –0.74 MPa in *A. aleuticum*. Evergreen species had P_{12} values from –0.42 MPa in *D. arguta* to –0.93 MPa in *P. munitum*, a similar range as the deciduous species. However, P_{50} values were lower in evergreen species (–5.63 to –7.2 MPa) than deciduous species (–0.74 to –2.81 MPa), indicating that evergreen ferns were more resistant to cavitation at moderate xylem water potential than ferns with shorter leaf lifespans. While deciduous species generally exhibited higher vulnerability to cavitation at low xylem water potentials, the xylem of *A. filix-femina* xylem was exceptionally vulnerable, reaching 100% loss of conductivity by –3.0 MPa. The evergreen ferns were not observed to reach 100% loss of conductivity at the lowest xylem water potential values measured, so the P_{88} values for these species were not reported.

The loss of xylem conductivity was estimated for each species *in situ* using the mid-day leaf water potentials measured in the field during summer, with the assumption that the leaf water potential gradient was minimal in these understory ferns (Fig. 2A). The plants were generally well hydrated and predicted PLC values ranged from 1.9% in *P. aquilinum* to 19.1% in *A. filix-femina,* while the highest PLC was predicted to be 16.5% in *D. arguta*. These low PLC values indicate that ferns maintain a significant buffer against drought-induced embolism since *in situ* PLC values are well below the 50% threshold.

DISCUSSION

The results of this study show that co-occurring evergreen and deciduous fern species share many foliar traits, but differ in leaf mass per area and resistance to drought-induced hydraulic cavitation at low water potentials. During midsummer when soil moisture is declining in the redwood forest (Burgess and Dawson 2004; Ewing et al. 2009), deciduous and evergreen fern species were both well hydrated at mid-day and had similar g_s within the range previously observed in other fern species (Brodribb et al. 2005; Watkins et al. 2010). While negligible rainfall occurred during the weeks before midsummer physiological measurement, maritime fog may have provided supplemental water (Oberlander 1956; Azevedo and Morgan 1974). These plants

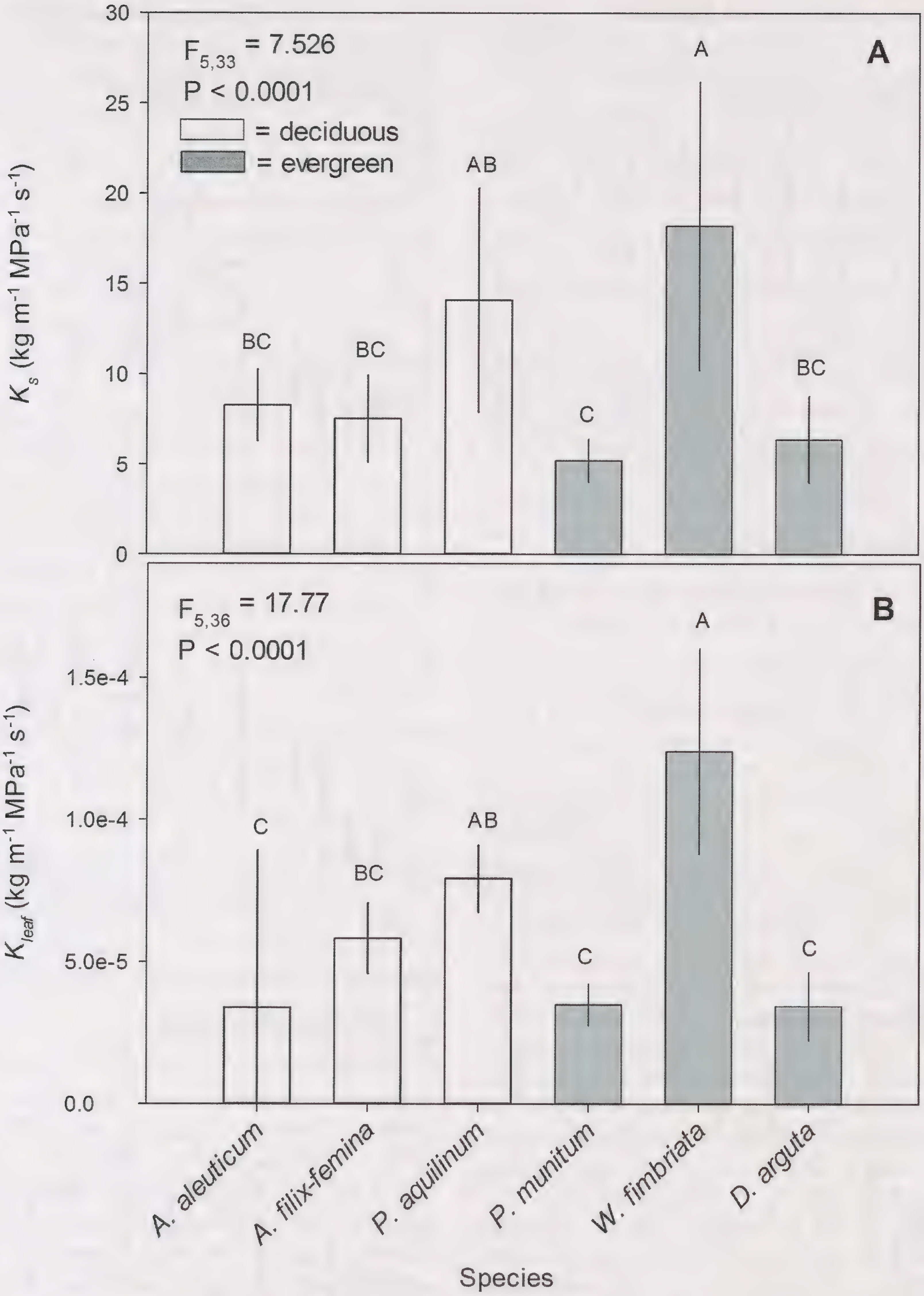

FIG. 5. A. The mean (±SD) xylem-specific conductivity (K_s) and B. mean (±SD) leaf-specific conductivity (K_{leaf}) from stipes of deciduous and evergreen species sampled at the Landels-Hill Big Creek Reserve (*Adiantum aleuticum*, *Pteridium aquilinum*, *Polystichum munitum*, and *Woodwardia fimbriata*) and University of California, Santa Cruz Natural Reserve (*Athyrium filix-femina* and *Dryopteris arguta*). Species with the same letter are not significantly different (Tukey's HSD, $\alpha = 0.05$).

would have become measurably less hydrated as the summer progressed, however such drought conditions trigger senescence in deciduous ferns and prevent the species comparisons studied here. In future studies, additional tools such as fluorimetry may be useful for identifying any differences in the earliest signs of drought response between evergreen and deciduous ferns, as was previously shown in north temperate fern species by Reudink et al. (2005).

The vulnerability curves showed that cavitation does in fact differ between evergreen and deciduous ferns. Estimated PLC values at the water potentials measured mid-day in the field were similar between all species, but the higher P_{50} values measured in the laboratory at milder xylem tensions in the deciduous species indicate that they are more susceptible to cavitation than their evergreen counterparts. This contrast was most striking between the evergreen fern, *W. fimbriata,* and deciduous fern, *A. filix-femina.* These two species commonly co-occur along perennially wet stream banks and yet *W. fimbriata* exhibited P_{50} = –5.63 MPa while *A. filix-femina* exhibited P_{50} = –0.74 MPa (Fig. 6). Apparent drought tolerance in *W. fimbriata* is consistent with

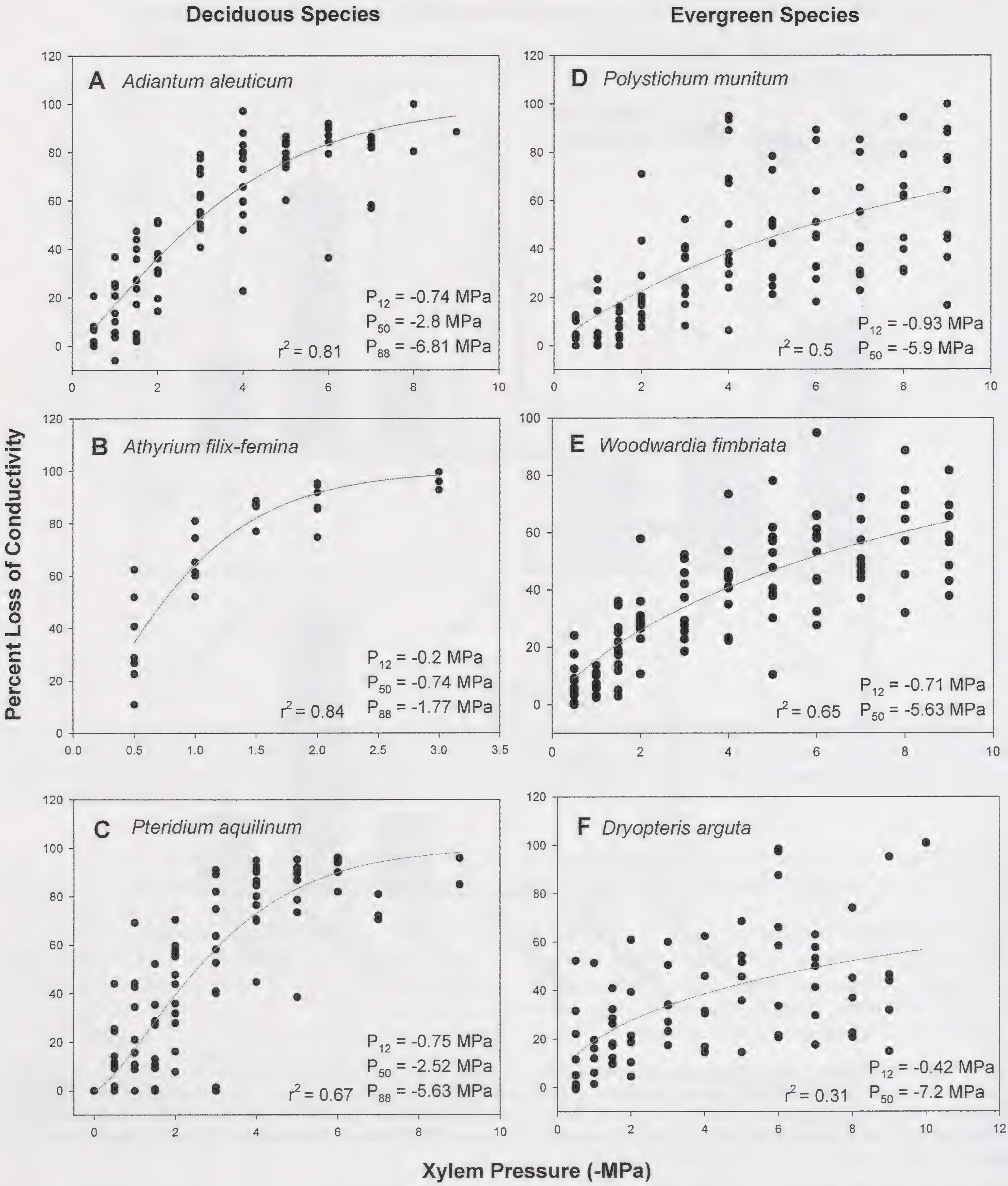

FIG. 6. The hydraulic response to increasingly negative xylem water potential in the frond stipes of A. *Adiantum aleuticum*, B. *Athyrium filix-femina*, C. *Pteridium aquilinum*, D. *Polystichum munitum*, E. *Woodwardia fimbriata*, and F. *Dryopteris arguta* for leaves sampled at the Landels-Hill Big Creek Reserve and University of California, Santa Cruz Natural Reserve. Vulnerability curves were obtained using the centrifugal method of Alder et al. (1997).

observations that this species can inhabit seasonally dry soils and establish further away from waterways than *A. filix-femina* (Burns and Pittermann personal observations). The higher vulnerability to cavitation in *A. filix-femina* may be a deciduous strategy, in which this species invests less carbon in xylem structure and avoids drought by senescing leaves in response to dropping water potentials (Brodribb and Holbrook 2004, 2005). While both species are observed to co-occur in the mesic coast redwood forest, differences in their phylogenetic lineages may also explain greater drought tolerance in *W. fimbriata*, a species with sister taxa in the Blechnaceae that occupy more xeric habitats (Smith et al. 2008).

The observed high resistance to cavitation in *W. fimbriata* and other evergreen species suggests that their preference for moist habitats is not likely due to stipe vulnerability to cavitation, and may be related to other traits. Indeed, one would expect the stipe to exhibit a high degree of cavitation resistance because this segment of the frond supplies water to the distal photosynthetic tissue. Previous studies have shown distal portions of the *W. fimbriata* frond to be significantly more sensitive to drought-induced cavitation than the stipe (Brodersen et al. 2012). In woody plants, drought sensitivity may be highest in distal plant parts such as roots and leaves, so similar segmentation may be occurring in ferns (Sperry and Ikeda 1997; Linton et al. 1998; Brodribb and Holbrook 2004). Altogether, this suggests that the stipe portion of *W. fimbriata* and other perennial ferns may have xylem that is more resistant to drought than required for the water potentials this species typically experiences *in situ* (Pittermann et al. 2011). This could be achieved via variable xylem arrangements (Brodersen et al. 2012; Pittermann et al. 2013) and high resistance to air entry into conduits (Brodersen et al. 2014). Despite occurring in generally mesic habitats, cavitation-resistant xylem may still provide an advantage to this species during extreme events such intense or prolonged droughts that would otherwise render the evergreen fern crown susceptible to hydraulic failure. Watkins et al. (2010) found that tropical epiphytic ferns had greater resistance to cavitation than terrestrial fern species which suggests we may find even higher drought tolerance in coast redwood forest ferns if we compare our study species with epiphytic ferns of the redwood forest canopy (e.g., *Polypodium scouleri* Hook. & Grev.; Sillett and Bailey 2003). Further research is needed to investigate greater contrasts between evergreen and deciduous species at more xeric margins of the species' natural range.

Deciduous ferns had significantly higher leaf area per mass than evergreen ferns, a trend commonly observed in among both seed-free and seed-bearing taxa (Merino et al. 1982; Aerts 1995; Givnish 2002; Karst and Lechowicz 2007). This is likely due to the fact that short-lived leaves do not have the same structural requirements needed to withstand biotic and abiotic stress over long periods of time (Chabot and Hicks 1982; Westoby et al. 2002). While carbon to nitrogen ratios and other leaf chemical constituents were not analyzed in this study, other studies suggest that deciduous leaves may be as costly to produce as evergreen species because plants invest more in photosynthetic proteins while investing less in protective structural and defensive chemicals (Merino et al. 1982; Aerts 1985). This variation in leaf allocation strategies may explain in part the absence of differences between evergreen and deciduous ferns with respect to stomatal conductance, a proxy for photosynthesis. Alternatively, there may be little need for dramatically different physiological strategies in a consistently cool and shady understory habitat of the redwood forest.

Given that deciduous ferns were neither larger nor observed losing more water at mid-day (exhibited similar g_s) than evergreen species in mid-summer, ferns with short-lived leaves may simply exhibit different phenological and life-history strategies in mesic habitats. Aerts (1995) suggests that deciduous species with leaves living for 9–10 months share similar foliar traits with leaves that live for 2–3 years. In addition, Sato (1990) found that summer green ferns often resemble evergreen species in the juvenile sporophyte stage. We know little about the recruitment strategies of each species but recruitment phenology may vary between evergreen and deciduous ferns, with seasonally deciduous taxa opportunistically recruiting in early summer, whilst perennial taxa have a broader moisture window. Investigating the drought tolerance of young sporophytes and the gametophyte life stages warrants further research.

In conclusion, co-occurring evergreen and deciduous species of the coast redwood forest exhibit similar physiology and hydraulic efficiency and differ most in leaf thinness and vulnerability to cavitation at low water potentials. It should be noted that this was a conservative study—one where the water was not limiting and future work in more water-limiting habitats or conditions may reveal even greater difference because evergreen and deciduous species. A recent study of seasonal water relations in *P. munitum* and *D. arguta* has shown that prolonged drought stress can induce severe losses of physiological function even in these drought-tolerant species (Baer et al. 2016), suggesting deciduous ferns are likely to be much more vulnerable to severe water deficit. Despite the perennials' ability to passively recover hydraulic conductivity following persistent water stress (Baer et al. 2016), the legacy effects on growth and fitness are poorly understood, and may have profound effects on the composition of the redwood forest understory. If California drought intensifies as temperature climbs in the decades ahead (Hayhoe et al. 2004; Loarie et al. 2009), our results will provide important *in situ* reference physiology data for these species that offer a baseline for comparison with future drought responses.

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